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Cretaceous winged stick insects clarify the early evolution of Phasmatodea

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Wingless and shorter winged stick insects are very common today, but most known extinct stick insects had fully developed wings, leading to contentious affinities among the extinct winged and extant groups. We report herein three male winged stick insects, assigned to Pterophasmatidae fam. nov., from mid-Cretaceous Myanmar (Burmese) amber. Pterophasmatidae fam. nov. are regarded as transitional taxa from extinct winged to modern wingless and shorter winged stick insects based on their similar tegmina venation with extinct Susumanioidea and some body features the same as extant Phasmatodea. However, their symmetric phallic organs comprising two consistent phallomeres are different from those of all living groups. Phylogenetic analyses suggest that the extinct winged taxa, including the new family, are the stem groups of modern stick and leaf insects, and all of them constitute the clade of Phasmatodea. New findings indicate winged and wingless stick insects' morphologies diversified significantly during or before the mid-Cretaceous.

1. Introduction

Phasmatodea, a rather small order of stick and leaf insects, comprise more than 3000 described extant species which are different from extinct winged groups. Just like their common names, they are remarkable mimics of the stems, twigs and leaves on which they live and feed [1–3]. At present, the classification system of Phasmatodea still remains questionable [4–7]. However, modern Phasmatodea comprise the Timematodea and the remaining Phasmatodea (= Euphasmatodea), which have been confirmed by many phylogenetic studies based on morphological characters or DNA sequence data [8–12].

The stick insects have a fairly poor fossil record [4,13,14], and the taxonomic positions of most fossil taxa remain uncertain because of the lack of informative characters visible or preserved. However, the extinct Susumanioidea Gorochov, 1988 have been interpreted to be true stem-group Phasmatodea and are probably paraphyletic with respect to the Euphasmatodea [13,14]. Nel & Delfosse [15] described *Renphasma* of Susumaniidae, which has a typical vomer of extant stick insects, supporting the hypothesis that these winged fossil taxa and modern stick insects belong to the same clade, but the exact relationship among these extinct winged and extant wingless and shorter winged stick insects still remains unclear.

Stick insects have been documented in Dominican amber [16–18], Mexican amber [19], Baltic amber [20], Oise amber [21] and Myanmar (Burmese) amber [4,22–24]. Most of these described amber species are wingless. Only two families, Archipseudophasmatidae and Gallophasmatidae, with fully developed wings have been reported from Baltic and Oise amber, respectively. Zompro [20] erected the family Archipseudophasmatidae based on some Eocene Baltic amber and described only two features of wing venation: radius vein branched in tegmina and 'shoulder' (same as 'knob-like dorsal eversion', a pronounced hump in the area between the radius and media (M) that could be correlated with the presence of a particular folding of the hind wing, described by Nel *et al*. [21]) of tegmina acute and projecting. Nel *et al*. [21] described another winged stick insect, *Gallophasma longipalpis* (Gallophasmatidae), from the earliest Oise amber in France, which has the same wing venation of tegmina as Archaeorthoptera. However, Bradler *et al*. [25] argued that *Gallophasma longipalpis* does not belong to the stem lineage of recent Phasmatodea.

Herein, we describe three winged stick insects, which have similar tegmina venation as some Susumanioidea and share some synapomorphies with extant groups, but male genitalia are different from all stick insects previously documented. Therefore, these new species provide morphological evidence for us to clarify the early evolution of Phasmatodea and the relationship among Phasmatodea, Embioptera and Orthoptera.

2. Results

(a) Systematic palaeontology

Order Phasmatodea Jacobson & Bianchi, 1902

Family Pterophasmatidae Yang, Shih, Ren & Gao fam. nov.

Type genus. *Pterophasma* Yang, Shih, Ren & Gao gen. nov.

Diagnosis. Fully winged in male; tegmina with 'knob-like dorsal eversion', without 'procostal' area, the branch location of radial posterior (RP) in distal of RP origin or RP unbranched, anal area narrow. Labrum emarginated; antennifer well-defined; antenna longer than profemora, with a prominence on the surface of pedicel base; third antennomere not especially elongate. Pronotum without lateral extension, with a distinctly transverse furrow on anterior part; metasternum and abdominal sternum I fused. Area apicalis present; five-segmented tarsi and with arolia. Abdominal tergum X divided; vomer absent; phallic organ symmetric and with two phallomeres; male with thorn pads in tergum X; cerci unsegmented and bipartite.

Included genera. *Pterophasma* gen. nov., *Leptophasma* gen. nov., *Meniscophasma* gen. nov.

Remarks. Pterophasmatidae fam. nov. are different from Archipseudophasmatidae which have the third antennomere at least twice as long as scapus and pedicellus combined, median segment longer than half length of metanotum and ocelli absent [20]. Pterophasmatidae fam. nov. are also different from Gallophasmatidae which have a pattern of tegmina venation typical of Archaeorthoptera, tegmina without 'knob-like dorsal eversion', area apicalis of tibia absent and maxillary palps very elongate (six-segmented) and much longer than head and cerci with four apparent 'segments' [21]. Although the tegmina venations of extinct Susumanioidea (e.g. *Adjacivena rasnitsyni* Shang, Béthoux & Ren, 2011, *Hagiphasma paradoxa* Ren, 1997, *Cretophasmomima melanogramma* Wang, Béthoux & Ren, 2014) are similar to those of Pterophasmatidae fam. nov. (figure 5), the male genitalia of Pterophasmatidae fam. nov. are different from those of Susumanioidea and living groups [13,26–28]. In addition, the phylogenetic analyses (figure 1) suggest that Susumanioidea are non-monophyletic, and *Renphasma* Nel & Delfosse, 2011 probably is not a genus of Susumanioidea. Furthermore, *Gallophasma* of Gallophasmatidae has a closer relationship with Orthoptera than with Phasmatodea, and *Archipseudophasma* of Archipseudophasmatidae has a closer relationship with Susumanioidea. Therefore, the internal relationships of these winged stick insects are still contentious, more well-preserved specimens are needed for future studies.

Genus *Pterophasma* Yang, Shih, Ren & Gao gen. nov.

Type species. *Pterophasma erromera* Yang, Shih, Ren & Gao sp. nov.

Etymology. The new generic name is a combination of the Greek '*ptero-*' meaning 'wing', and '*phasma*', stem of the ordinal name of Phasmatodea. The name refers to the fully winged stick insects. The gender is feminine.

Diagnosis. Tegmina with RP two branches, CuA + CuPaα (see figure 5 caption for definitions of venation) two distal branches, two anal veins and anal area with cross-veins. Three ocelli present. Metafemur thickened and with a spine at the base of hind tibiae; all area apicalis without spines; all tarsi with euplantulae. Subgenital plate with two large lobes at the terminal; abdominal tergum X with only two teeth on both sides; phallic organ with broad phallomeres and cerci bifurcated in a basal position, one straight and the other curved inward.

Pterophasma erromera Yang, Shih, Ren & Gao sp. nov. (figure 2 and figure 5*f*)

Etymology. The epithet is from the Latin word '*erromerus*', referring to the tibia of hind leg which is thick and strong.

Diagnosis. As for the genus.

Holotype. An adult male, no. BU-001438.

Type locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) of northern Myanmar, which was dated at 98.79 ± 0.62 Ma [29,30].

Description. See the electronic supplementary material, data S1 for a complete description.

Genus *Leptophasma* Yang, Shih, Ren & Gao gen. nov.

Type species. *Leptophasma physematosa* Yang, Shih, Ren & Gao sp. nov.

Etymology. The new generic name is a combination of the Greek '*lepto-*' meaning 'slender', and '*phasma*', stem of the ordinal name of Phasmatodea. The name refers to the slender legs, thorax and abdomen. The gender is feminine.

Diagnosis. Tegmina with radial anterior (RA) subbranch, RP two short branches, CuA + CuPaα two long branches, an anal vein and anal area without cross-veins. Ocelli absent; scape of antenna large and swollen at terminal. Prothorax elongate, length twice the width. All legs slender, profemora slightly curved near base. The terminal part of abdomen not preserved.

Leptophasma physematosa Yang, Shih, Ren & Gao sp. nov. (figure 3 and figure 5e)

Etymology. The epithet is from the Latin word '*physematosus*', referring to the scape of antenna which is swollen.

Diagnosis. As for the genus.

Holotype. An adult male, no. CNU-PHA-MA2018005.

Type locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) of northern Myanmar, which was dated at 98.79 ± 0.62 Ma [29,30].

Description. See the electronic supplementary material, data S2 for a complete description.

Genus *Meniscophasma* Yang, Shih, Ren & Gao gen. nov.

Type species. *Meniscophasma erythrosticta* Yang, Shih, Ren & Gao sp. nov.

Etymology. The new generic name is a combination of the Greek '*menisco-*', meaning 'crescent-shaped', and '*phasma*', stem

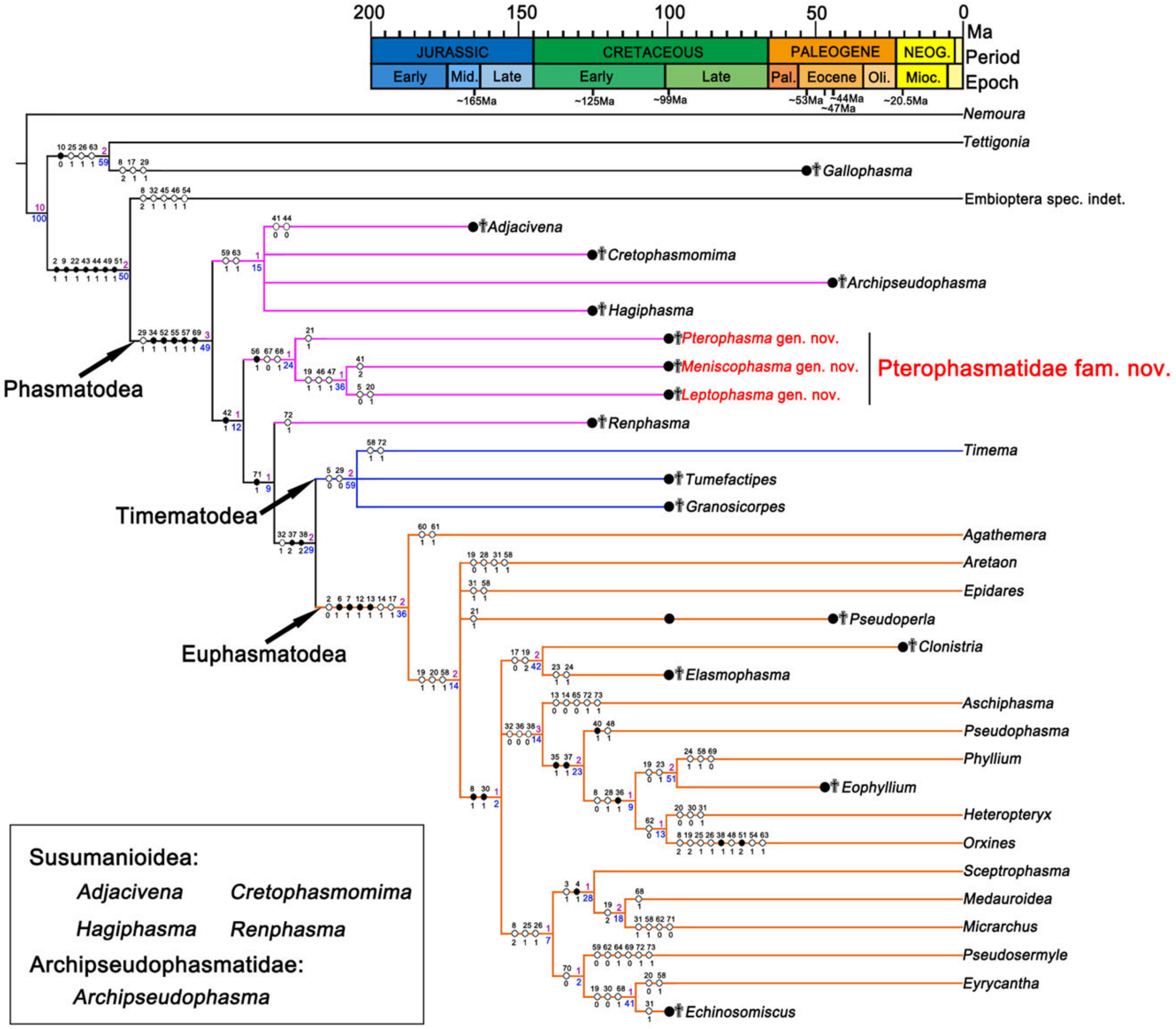

Figure 1. Phylogeny of Phasmatodea based on morphological characters. The strict consensus tree, tree length = 187 steps, consistency index (CI) = 0.44, retention index (RI) = 0.66. The numbers under the branch nodes are bootstrap support values (data in blue) and the numbers on the branch nodes are Bremer support values (data in purple). The large black dots show the age of the genera, and the branch nodes of this strict consensus tree do not represent any time. Small black dots, unambiguous unique characters; small white dots, homoplasious characters. (Online version in colour.)

of the ordinal name of Phasmatodea. The name refers to the crescent-shaped abdominal tergum X. The gender is feminine.

Diagnosis. Tegmina with RP unbranched, CuA + CuPaα two long branches; one anal vein and anal area without cross-veins. With a protuberance on head; three ocelli present and antenna much longer than profemur but shorter than body. Femora of hind legs apparently slightly curved. Subgenital plate with two small lobes at terminal; abdominal tergum X elongate and crescent-shaped, respectively; phallic organ with elongated phallomeres and cerci bifurcated nearly at the middle.

Meniscophasma erythrosticta Yang, Shih, Ren & Gao sp. nov. (figures 4 and 5*g*)

Etymology. The epithet is from the Latin word '*erythrostictus*', referring to the regular red spots of all the femora.

Diagnosis. As for the genus.

Holotype. An adult male, no. BU-001967.

Type locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) of northern Myanmar, which was dated at 98.79 ± 0.62 Ma [29,30].

Description. See the electronic supplementary material, data S3 for a complete description.

(b) Phylogenetic analyses

Our phylogenetic analyses, based on morphological characters, produced a strict consensus tree (figure 1) and two most parsimonious trees (electronic supplementary material, figure S1 using WinClada and electronic supplementary material, figure S2 using TNT). Although the support values (bootstrap and Bremer support, electronic supplementary material, figure S3) are low probably owing to the absence of many detailed features in fossils and wing venation features in extant stick insects, the following unquestionable results can be obtained.

The strict consensus tree (figure 1) indicates the extinct winged Susumanioidea, Archipseudophasmatidae and Pterophasmatidae fam. nov. belong to Phasmatodea, together with Timematodea and Euphasmatodea form the clade Phasmatodea. The monophyly of Phasmatodea is supported by five synapomorphies: 'knob-like dorsal eversion' of tegmina present (character 34: 1), cubitus (Cu) of hind wing unbranched or without Cu (character 52: 1), 2–7A of hind wing with a common origin at the wing base (character 55: 1), cerci unsegmented (character 57: 1), males with thorn pads in tergum X (character

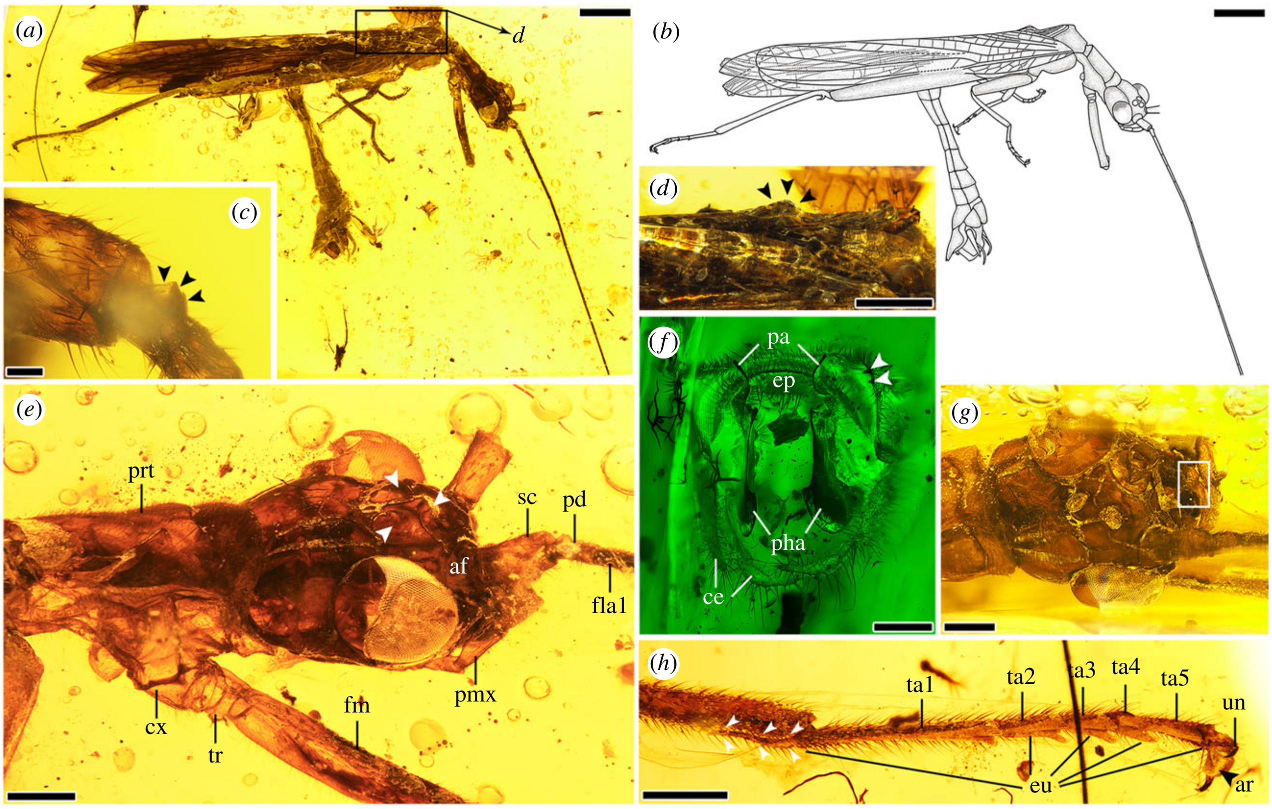

Figure 2. Photographs of *Pterophasma erromera* gen. et sp. nov. (BU-001438) (*a*) Lateral view as preserved. (*b*) Line drawing of lateral view. (*c*) Right antenna, a tubercle on surface of pedicel base (black arrows). (*d*) The 'knob-like dorsal eversion' of tegmina (black arrows). (*e*) Head in lateral view, three ocelli (white arrows). (*f*) Male genital photograph in posterior view, thorn pad (white arrows), under green fluorescent protein (GFP) mode. (*g*) Head in dorsal view, showing labrum (white wireframe). (*h*) Right metatarsus in lateral view, showing the area apicalis (white arrows) of right metatibia. Scale bars: (*a,b,d*), 2 mm; (*c*), 0.1 mm; (*e,g–h*), 0.5 mm; (*f*), 0.4 mm. af, antennal field; ar, arolium; ce, cercus; cx, coxa; ep, epiproct; eu, euplantula; fla1, flagellomere I; fm, femur; pa, paraproct; pd, pedicellus; pha, phallomeres; pmx, maxillary palpus; prt, pronotum; sc, scape; ta1–ta5, tarsomeres I–V; tr, trochanter; un, claw. (Online version in colour.)

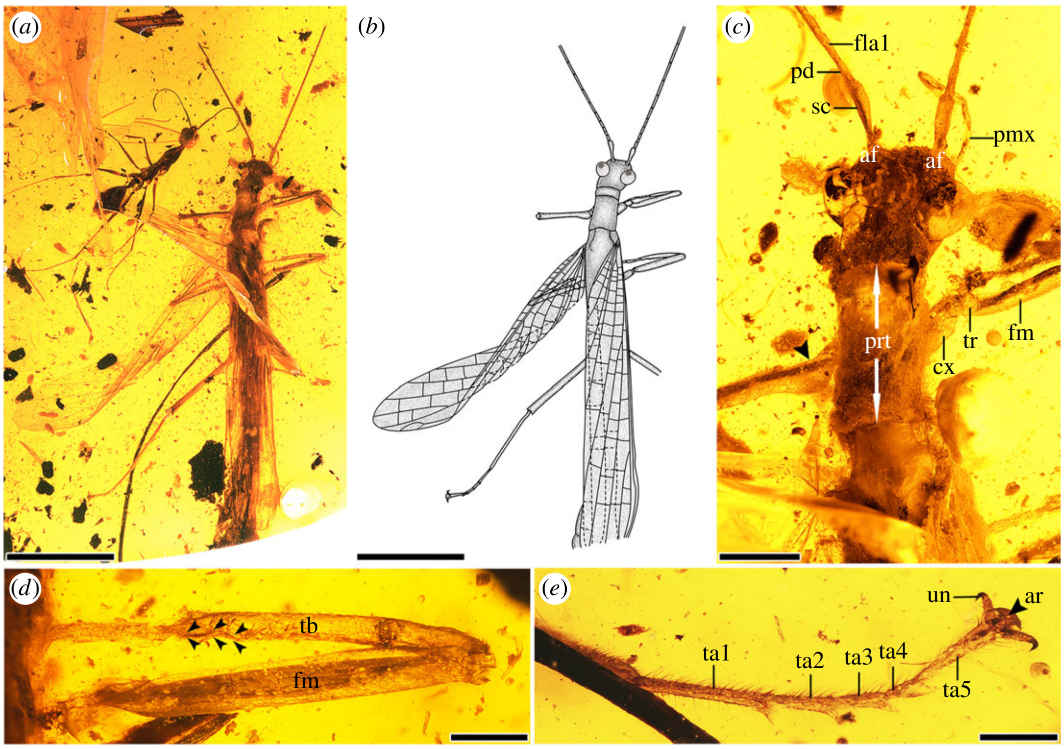

Figure 3. Photographs of *Leptophasma physematosa* gen. et sp. nov. (CNU-PHA-MA2018005) (*a*) Dorsal view as preserved. (*b*) Line drawing of dorsal view. (*c*) Head in dorsal view, profemora curved (black arrows). (*d*) Right middle leg, showing area apicalis (black arrows) of right mesotibia. (*e*) Left protarsus in ventral view. Scale bars: (*a–c*), 5 mm; (*d–e*), 0.5 mm. af, antennal field; ar, arolium; cx, coxa; fla1, flagellomere I; fm, femur; pd, pedicellus; pmx, maxillary palpus; prt, pronotum; sc, scape; ta1–ta5, tarsomeres I–V; tb, tibia; tr, trochanter; un, claw. (Online version in colour.)

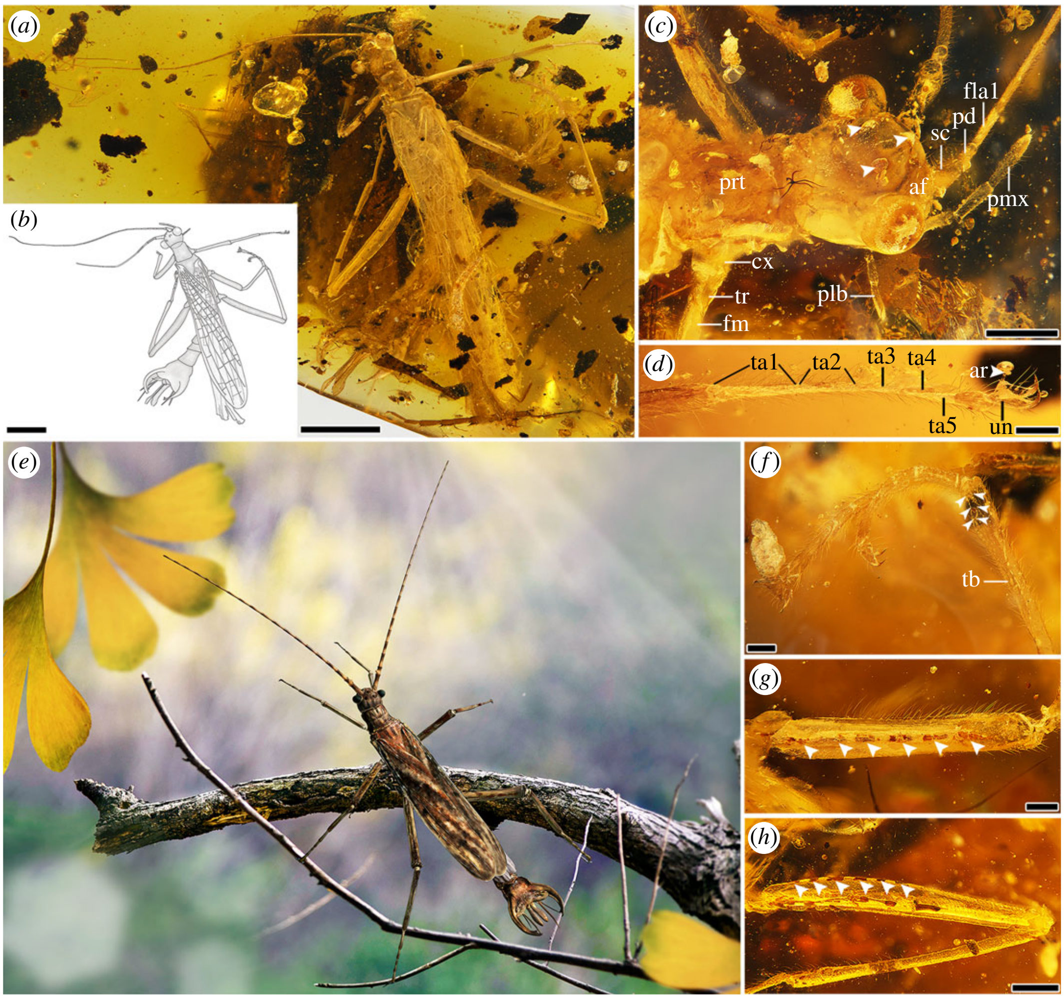

Figure 4. Photographs of *Meniscophasma erythrosticta* gen. et sp. nov. (BU-001967) (*a*) Dorsal view as preserved. (*b*) Line drawing of dorsal view. (*c*) Head in dorsal view, three ocelli (white arrows). (*d*) Right protarsus in dorsal view. (*e*) Three-dimensional ecological reconstruction of *Meniscophasma erythrosticta* gen. et sp. nov. (*f*) Right meso- and metatarsus in lateral view, showing area apicalis (white arrows) of right mesotibia. (*g*) Right mesofemur, showing red spots (arrows). (*h*) Right metafemur, showing red spots (arrows). Scale bars: (*a,b*), 2 mm; (*c*), 0.5 mm; (*d,f–g*), 0.2 mm; (*h*), 0.5 mm. af, antennal field; ar, arolium; cx, coxa; fla1, flagellomere I; fm, femur; pd, pedicellus; plb, labial palpus; pmx, maxillary palpus; prt, pronotum; sc, scape; ta1–ta5, tarsomeres I–V; tb, tibia; tr, trochanter; un, claw. (Online version in colour.)

69: 1) and a homoplasious character, tarsus with five articles (character 29: 1). Although Timematodea have a trimerous tarsus, it is formed by the first three tarsomeres of the originally five-segmented tarsus fused, so the five-segmented tarsus is a plesiomorphy of Phasmatodea [5,8,9,12].

The monophyly of Pterophasmatidae fam. nov. is supported by a synapomorphy and two homoplasious characters: cerci bipartite (character 56: 1), genitalia (phallic organ of abdominal segment IX) symmetric (character 67: 0) and the abdominal tergum X of male split (character 68: 1). Furthermore, Pterophasmatidae fam. nov. share some apomorphies with living groups: labrum emarginated [5,9,31], antennifer well-defined [5,8,9], metasternum and abdominal sternum I fused [5,23–25], male with thorn pads in tergum X [5,14] and cerci unsegmented [5,8,32]. Therefore, Pterophasmatidae fam. nov. is definitely a stem-group of Phasmatodea.

Based on the results of our phylogenetic analyses (figure 1), Phasmatodea are corroborated to have a closer relationship with Embioptera than with Orthoptera, the apomorphies of Phasmatodea with Embioptera are as follows: antennifer well-defined (character 2: 1), prothorax without lateral extension (character 9: 1), trochanter fused with the femur (character 22: 1), media (M) of tegmina with two branches (character 43: 1), the branch location of M in behind of RP origin (character 44: 1), RP of hind wings unbranched (character 49: 1) and M of hind wings with two branches (character 51: 1).

3. Discussion

(a) Phylogenetic position of Pterophasmatidae fam. nov

To date, stick insects from Myanmar (Burmese) amber have been described based on apterous adults and nymphs, and they are all recognized as true stick insects [4,22–24]. Here, we described three winged adults for the first time, *Pterophasma erromera* gen. et sp. nov., *Meniscophasma erythrosticta* gen. et sp. nov. and *Leptophasma physematosa* gen. et sp. nov. from the same deposit. They have fully developed wings and a pattern of tegmina venation similar to those of the species of Susumanioidea from the Middle Jurassic to Eocene [28,33], such as the tegmina not abbreviated and slightly shorter than hind wings at rest, without the 'precostal' area, proximal origin of RP, M with two branches and Cu with several branches (figure 5). Therefore, these three new genera are much more similar to Susumanioidea than living groups, which is consistent with our phylogenetic analyses (figure 1). However, Pterophasmatidae fam. nov. have well-developed antennifer of their antennae exhibited by Embioptera and Timematodea, which suggests that

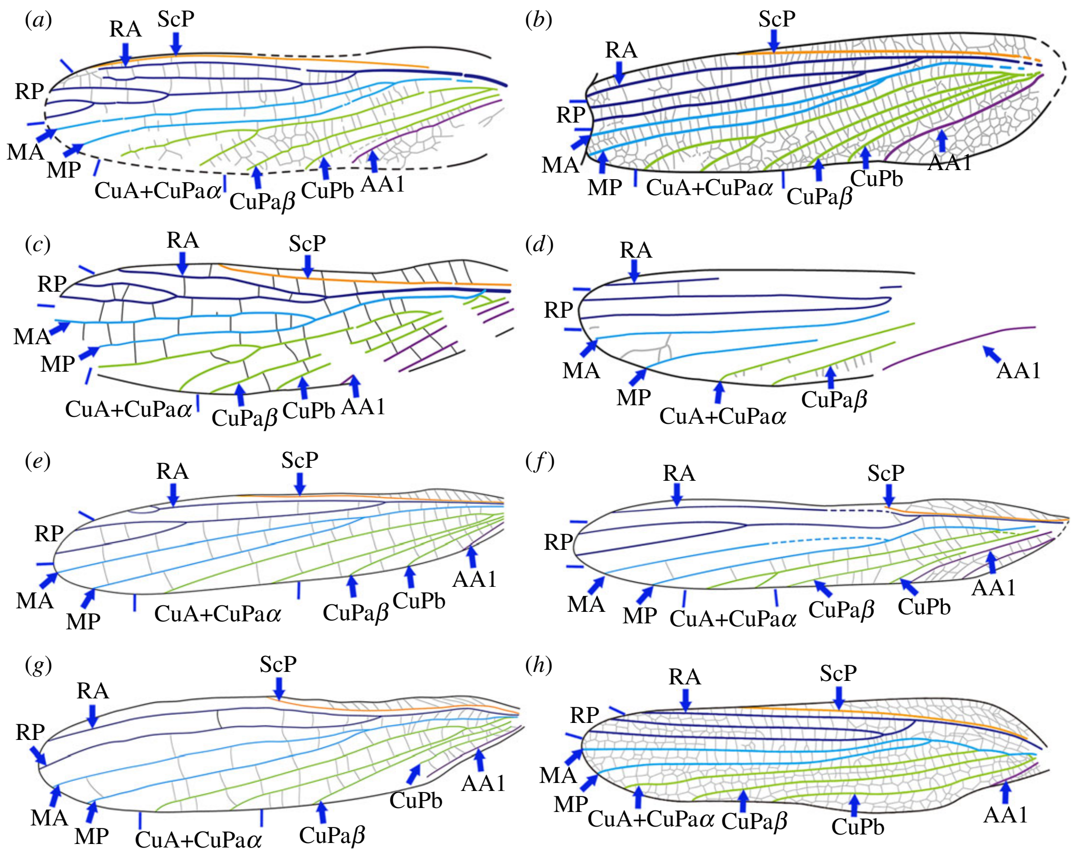

Figure 5. Comparisons for line drawings of tegmina venation. (*a*) *Adjacivena rasnitsyni* Shang, Béthoux & Ren, 2011. (*b*) *Hagiphasma paradoxa* Ren, 1997. (*c*) *Renphasma sinica* Nel & Delfosse, 2011. (*d*) *Cretophasmomima melanogramma* Wang, Béthoux & Ren, 2014. (*e*) *Leptophasma physematosa* gen. et sp. nov. (*f*) *Pterophasma erromera* gen. et sp. nov. (*g*) *Meniscophasma erythrosticta* gen. et sp. nov. (*h*) *Heteropteryx dilatata* Parkinson, 1798. AA1, anterior anal vein; Cu, cubitus; CuA, cubital anterior; CuP, cubital posterior; CuPa, anterior branch of CuP; CuPaα, anterior branch of CuPa; CuPaβ, posterior branch of CuPa; CuPb, posterior branch of CuP; M, media; MA, medial anterior; MP, medial posterior; R, radius; RA, radial anterior; RP, radial posterior; ScP, subcostal posterior. (Online version in colour.)

Pterophasmatidae fam. nov. is a stem-group of Phasmatodea and different from Euphasmatodea with antennifer largely reduced [5,9]. The scape of *L. physematosa* gen. et sp. nov. is large and swollen at the apex as also found in Timematodea [8]. In addition, labrum emarginated and metasternum fused with the abdominal sternum I are the synapomorphies exhibited by all extant Phasmatodea but absent in Embioptera and most of Orthoptera, which also suggest Pterophasmatidae fam. nov. should be a stem-group of Phasmatodea. Moreover, there are many other body characters present in Pterophasmatidae fam. nov. and some living groups, such as three ocelli, area apicalis, arolia, euplantulae and 'knob-like dorsal eversion' of tegmina (figure 2*d*). All extant male winged Euphasmatodea have a more or less pronounced 'knob-like dorsal eversion' in tegmina [21], also present in Archipseudophasmatidae [20] and *Cretophasmomima melanogramma* Wang, Béthoux and Ren, 2014 (interpreted as 'shoulder pad') of Susumanioidea [13]. Therefore, we think that the 'knob-like dorsal eversion' of tegmina probably constitutes a synapomorphy of winged stick insects. In summary, we suggest that Pterophasmatidae fam. nov. are the transitional taxa from Susumanioidea to modern Phasmatodea.

(b) Wing evolution in stick insects

Many known groups of Susumanioidea were identified based on wings only, resulting in the questionable systematic position of Susumanioidea. Our phylogenetic results indicate that the supposed 'Susumanioidea' group should be assigned to Phasmatodea, though their internal relationship has not been adequately addressed here. *Heteropteryx dilatata* Parkinson, 1798, as the representative of extant winged stick insects, also have the tegmina not shortened and RP with two branches (figure 5*h* and the electronic supplementary material, figure S4) [12,21], but tegmina much shorter than hind wings at rest. Based on the tegmina of *Adjacivena* (the earliest fossil records of Susumanioidea from the Middle Jurassic, figure 5*a*) having multi-branched RP, which are in contrast to one to three branches in other Susumanioidea, Pterophasmatidae fam. nov. and *Heteropteryx dilatata*, it is suggested that the RP of tegmina have a tendency to decrease in number of branches within winged stick insects. Furthermore, the anal areas of *Adjacivena* and *Hagiphasma* (figure 5*a*,*b*) being wider than those of Pterophasmatidae fam. nov. (figure 5*e*–*g*) and *Heteropteryx dilatata* (figure 5*h*) also suggest that the anal areas of tegmina probably gradually shrank in the evolutionary process. All extinct winged stick insects have well-developed tegmina, but the tegmina of extant stick insects are shorter or absent. Although *Heteropteryx dilatata* has similar venation, the tegmina has a clear shortening trend compared with extinct winged stick insects. There are no documented fossils of stick insects with shorter wings except for *Eophyllium* Wedmann, Bradler & Rust, 2007 from Eocene [34]. All the known specimens of winged stick insects found before the mid-Cretaceous possessed long tegmina, such as Susumanioidea. Therefore, we suppose that the forewing shortening

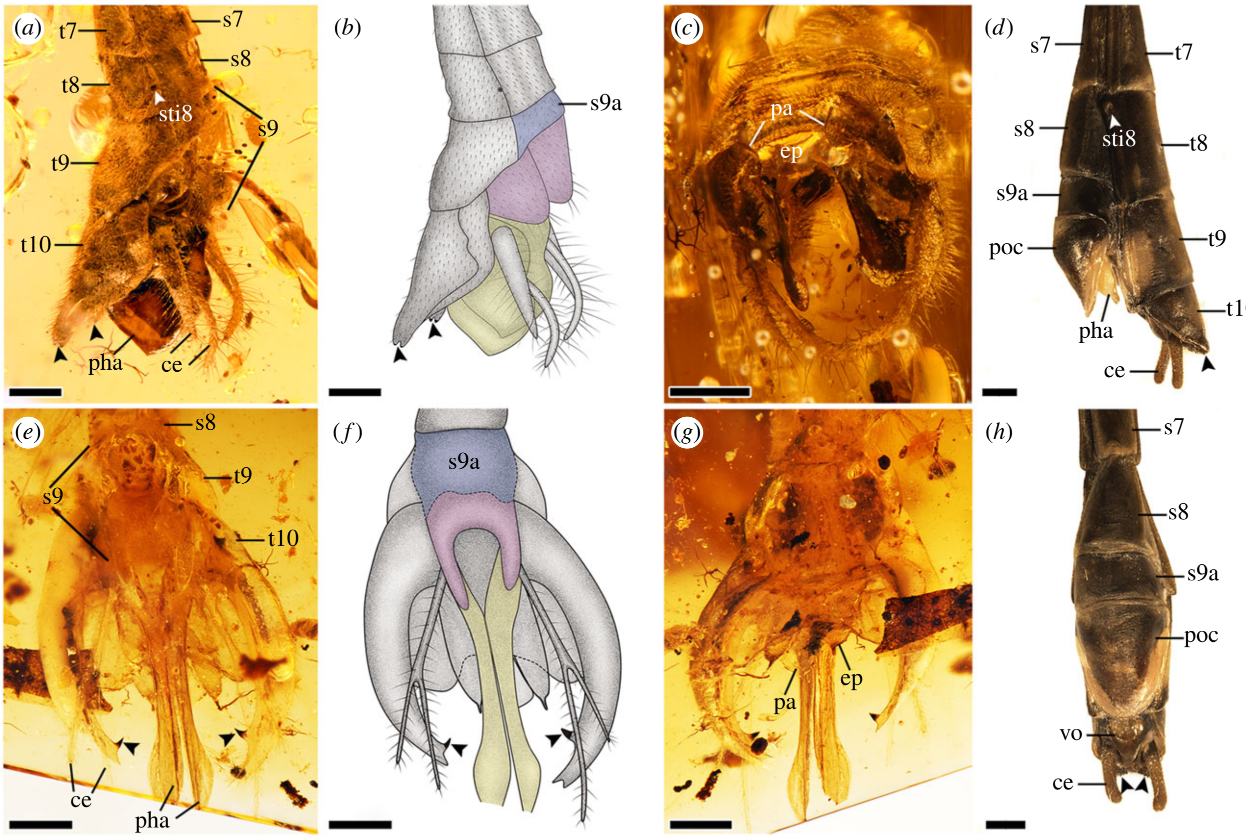

Figure 6. Male genitalia compared with modern stick insects. (*a*) Photograph of male genitalia of *Pterophasma erromera* gen. et sp. nov. in lateral view, thorn pads (black arrows). (*b*) Line drawing of male genitalia of *P. erromera* gen. et sp. nov., thorn pads (black arrows). (*c*) Photograph of male genitalia of *P. erromera* gen. et sp. nov. in posterior view. (*d*) Photograph of male genitalia of *Sipyloidea amica* (Bei-Bienko, 1959) in lateral view, thorn pads (black arrow). (*e*) Photograph of male genitalia of *Meniscophasma erythrosticta* gen. et sp. nov. in ventral view, thorn pads (black arrows). (*f*) Line drawing of male genitalia of *M. erythrosticta* gen. et sp. nov., thorn pads (black arrows). (*g*) Photograph of male genitalia of *M. erythrosticta* gen. et sp. nov. in dorsal view. (*h*) Photograph of male genitalia of *S. amica* (Bei-Bienko, 1959) in ventral view, thorn pads (black arrows). Scale bars: (*a–c*,*e–g*), 0.5 mm; (*d*,*h*), 1 mm. ce, cercus; ep, epiproct; pa, paraproct; pha, phallomeres; poc, poculum; s7–s9, sternum VII–IX; s9a, the anterior sternite of sternum IX; t7–t10, terga VII–X; vo, vomer. (Online version in colour.)

within stick insects might have occurred between the mid-Cretaceous and Eocene (99 ~ 47 Ma). However, many wingless stick insects in mid-Cretaceous Myanmar amber have been reported recently, showing a variety of body shapes [4,22,23,24]. Whiting [11] documented that the loss and recovery of wings in stick insects should have happened many times during the course of evolution based on abundant molecular data. In addition, the new findings and the phylogenetic analyses including fossil, extant, winged and wingless stick insects based on morphological features also corroborate that independent transitions from a winged form to winglessness have occurred more than once.

For a long time, the exact phylogenetic relationship of Phasmatodea with other polyneopteran lineages, especially Orthoptera and Embioptera, have always been contentious [4,10,11,24]. Our results of the phylogenetic analyses including some wing venation characters corroborate that Phasmatodea, including fossils, have a closer relationship with Embioptera than with Orthoptera. The closer relationship of Phasmatodea with Embioptera have also been confirmed by many other phylogenetic studies based on morphological characters or DNA sequence data [5,9–11,35,36].

(c) Evolution of the male genitalia within Phasmatodea

In males of living groups, distinctive morphological features mainly concern the abdominal sternum IX (subgenital plate) and the abdominal segment X, especially the venter X is particularly modified with specialized clasping organs involved in copulation [37]. In general, the abdominal subgenital plate of *Timema* and most Euphasmatodea is transversally divided into an anterior sternite and a posterior sternite (the poculum) and covered the phallic organ (e.g. *Sipyloidea amica* Bei-Bienko, 1959, figure 6*d*,*h* and electronic supplementary material, figure S5) [5,37]. A similar character also occurs in *P. erromera* gen. et sp. nov. and *M. erythrosticta* gen. et sp. nov. (figure 6*a*,*b*,*e*,*f*, denoted in blue and purple). The difference is the apical part of the subgenital plate splitting into two lobes (figure 6*b*,*f*, denoted in purple) rather than the poculum. We conjecture that these two lobes might have been used to enhance the male's control ability during copulation. Relatively, in most extant stick insects, the vomer is a hook-shaped, sclerotized derivative of the tenth sternum (e.g. *Sipyloidea amica* Bei-Bienko, 1959, figure 6*h*) that clasps the posterior margin of female sternum 7 to enhance the male's control [38,39]. Furthermore, the incurved and rather elongated cerci also play an important role in the mating [37]. The male of *P. erromera* gen. et sp. nov. has a incurved cerci (figures 2*f* and 6*a–c*), which is also present in extant and fossil stick insects *Renphasma sinica* Nel & Delfosse, 2011 [15]. Nevertheless, the tergum X of *M. erythrosticta* gen. et sp. nov. forms a pair of curved claspers behind the cerci (figure 6*e–g*), the claspers contain a pair of thorn pads (figure 6*e*,*f*, arrows), which might be used to enhance the male's control during copulation (similar to most extant Euphasmatodea) [5,40]. The presence of thorn pads on the hind margin of abdominal tergum X is one of the diagnostic characteristics of Euphasmatodea [5], and also present in *P. erromera* gen. et sp. nov. (figures 2*f*, 6*a*,*b*).

The male genital structures of stick insects frequently show greater divergence than female structures [41,42]. In many groups of Polyneoptera, the true male genitalia (phallic organs of abdominal segment IX) have highly complicated structures. In some Plecoptera, Blattaria, Mantodea, Phasmatodea and Orthoptera, the primary phallic organ comprises two to nine phallomeres located around the ejaculatory duct opening [43]. The male phallic organ of *Grylloblatta* (Grylloblattidae, Notoptera) comprises essentially two phallomeres, with the gonopore between them, or on the base of the right one [38]. Similarly, *P. erromera* gen. et sp. nov. and *M. erythrosticta* gen. et sp. nov. have symmetric phallic organs that contain two consistent phallomeres (figure 6*a*,*b*, *e*,*f*, denoted in yellow); however, the phallic organs of living groups are asymmetric. In Embioptera, the phallic organs are usually absent or little-developed. In Dictyoptera, Grylloblattodea and Mantophasmatodea, the phallic organs are also asymmetric and distinctly different between the left and right parts. Orthoptera usually have very complicated but symmetric phallic organs (though minor asymmetries may occur) [44]. It is supposed that a symmetric phallic organ might be a plesiomorphy for Phasmatodea.

(d) Diversified evolution of stick insects in the Cretaceous

Stick insects already have a broad diversity of morphological characters in mid-Cretaceous Myanmar amber (shown in figure 1), for example, winged Pterophasmatidae fam. nov., robust and compressed *Echinosomiscus primoticus* Engel, Wang & Alqarni, 2016 bearing abundant acanthae over the body [4], *Elasmophasma stictum* Chen, Yin, Shih & Ren, 2018 with well-preserved, thin, lateral lamellae on the thorax, the terga of abdomen and the ventrolateral margins of all femora [23], *Pseudoperla leptoclada* Chen, Zhang, Shih & Ren, 2017 with antenna slender and long [22], robust *Tumefactipes prolongates* Chen, Shih, Ren & Gao, 2018 and *Granosicorpes lirates* Chen, Shih, Ren & Gao, 2018 similar to *Timema* [24]. These specimens provide a minimal age for the origin and diversification of Timematidae and Euphasmatodea, and indicate the differentiation of winged and wingless stick insects occurred during or before the mid-Cretaceous. Therefore, the mid-Cretaceous is an important period of radiation and evolution for stick insects, which might be related to the extensive radiation of angiospermous diversity during this period [45].

4. Material and methods

(a) Specimens imaging and terminology

All amber type specimens described here are housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). However, BU-001438 and BU-001967 will eventually be deposited in the Three Gorges Entomological Museum, Chongqing (specimens to be available for study by contacting D.R. or W.W.Z.).

The amber specimens were examined under a Leica M205C dissecting microscope. All yellow and white background photographs were taken with a Nikon SMZ 25 microscope with an attached Nikon DS-Ri2 digital camera system and a Nikon ECLIPSE Ni microscope with an attached Nikon DS-Ri2 digital camera system. The green background photograph was taken with the Zeiss ApoTome.2 with an AXIO Zoom.V16 digital camera system under green fluorescent protein (GFP) mode. Line drawings were prepared by using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

The wing venation nomenclature follows Wang *et al*. [13]. The following abbreviations have been used throughout: AA1, anterior anal vein; Cu, cubitus; CuA, cubital anterior; CuP, cubital posterior; CuPa, anterior branch of CuP; CuPaα, anterior branch of CuPa; CuPaβ, posterior branch of CuPa; CuPb, posterior branch of CuP; M, media; MA, medial anterior; MP, medial posterior; R, radius; RA, radial anterior; RP, radial posterior; ScP, subcostal posterior.

(b) Phylogenetic analyses

We carried out phylogenetic analyses by using morphological characters to confirm the taxonomic position of Pterophasmatidae fam. nov. and to clarify phylogenetic relationships among Susumanioidea, Pterophasmatidae fam. nov., Timematodea and Euphasmatodea. Seventeen extant genera and 16 fossil genera are used in this analysis. For most extant genera, we chose the type genera as representatives, such as *Aschiphasma* Westwood, 1834, and for those groups without well-preserved type genera, we chose other representative genera instead, but all extant genera are attributable to Bradler's study in 2009 [5]. We added 13 fossil genera (*Renphasma* Nel & Delfosse, 2011 [15]; *Hagiphasma* Ren, 1997 [27]; *Adjacivena* Shang, Béthoux & Ren, 2011 [26]; *Cretophasmomima* Kuzmina, 1985 [13]; *Archipseudophasma* Zompro, 2001 [20]; *Gallophasma* Nel, Delfosse & Robillard, 2010 [21]; *Tumefactipes* Chen, Shih, Ren & Gao, 2018 [24]; *Granosicorpes* Chen, Shih, Ren & Gao, 2018 [24]; *Pseudoperla* Berendt & Pictet, 1854 [22]; *Clonistria* Stal, 1875 [17]; *Elasmophasma* Chen, Yin, Shih & Ren, 2018 [23]; *Eophyllium* Wedmann, Bradler & Rust, 2007 [34]; *Echinosomiscus* Engel, Wang & Alqarni, 2016 [4]) which have a relatively complete body, and three new genera of Pterophasmatidae fam. nov. (*Pterophasma* gen. nov., *Meniscophasma* gen. nov. and *Leptophasma* gen. nov.). To sum up, the phylogenetic analyses include 33 taxa with 30 ingroups and three outgroups of *Nemoura* Latreille, 1796 (Plecoptera), *Tettigonia* Linnaeus, 1758 (Ensifera), and Embioptera spec. indet., based on the study of Bradler, 2009 [5]. Meanwhile, we made some changes of the character states to enhance our analyses, most of the body characters are attributable to Bradler's study in 2009 and added some wing venation characters. A total of 73 morphological characters are shown in the electronic supplementary material, table S1, some are clearly present in three new genera, and others are important features of representative ingroups. The character-state matrix consisting of 33 taxa and 73 morphological characters is shown in the electronic supplementary material, table S2.

Parsimony analyses were performed by using WinClada (version 1.00.08) [46] and NONA (version 2.0) [47]. Tree search implemented a heuristic search method and the options were set to hold 10 000 trees, 1000 replications, 100 starting tree replications and a multiple TBR + TBR search strategy. All characters were considered unordered and weighted equally. Bootstrap supporting values were determined by using NONA with 1000 replications and are represented as numbers under the branch nodes (figure 1 and electronic supplementary material, figure S3a, data in blue). An analysis was run again in TNT (version 1.5) [48] with traditional search and the minimum length was set to be found 1000 times, an identical strict consensus tree was obtained. Bremer supporting values were calculated through the script 'bremer.run' of the program and are represented as numbers above the branch nodes (figure 1 and electronic supplementary material, figure S3b, data in purple).

Data accessibility. The datasets supporting the conclusions of this article are included within the article, and electronic supplementary material, figures S1–S5, description of three species, primary data of phylogenetic analyses, character matrix in nexus format is available in the electronic supplementary material.

Authors' contributions. T.P.G. and D.R. conceived and designed the experiments; H.R.Y., X.C.Y., X.D.L., C.W., C.K.S., W.W.Z., D.R. and T.P.G. performed the analyses and experiments; H.R.Y. prepared photographs and line drawings; C.W. prepared the three-dimensional ecological reconstruction artwork. H.R.Y., X.D.L., C.K.S., D.R. and T.P.G. wrote the manuscript. All authors read and approved the final manuscript.

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Electronic Supplementary Material for:

Cretaceous winged stick insects clarify the early evolution of Phasmatodea

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Figure S1. Phylogeny of Phasmatodea by using WinClada (Version1.00.08) and NONA (Version 2.0). (•) Unambiguous unique characters; (◦) Homoplasious characters.

Figure S2. Phylogeny of Phasmatodea by using TNT (Version1.5).

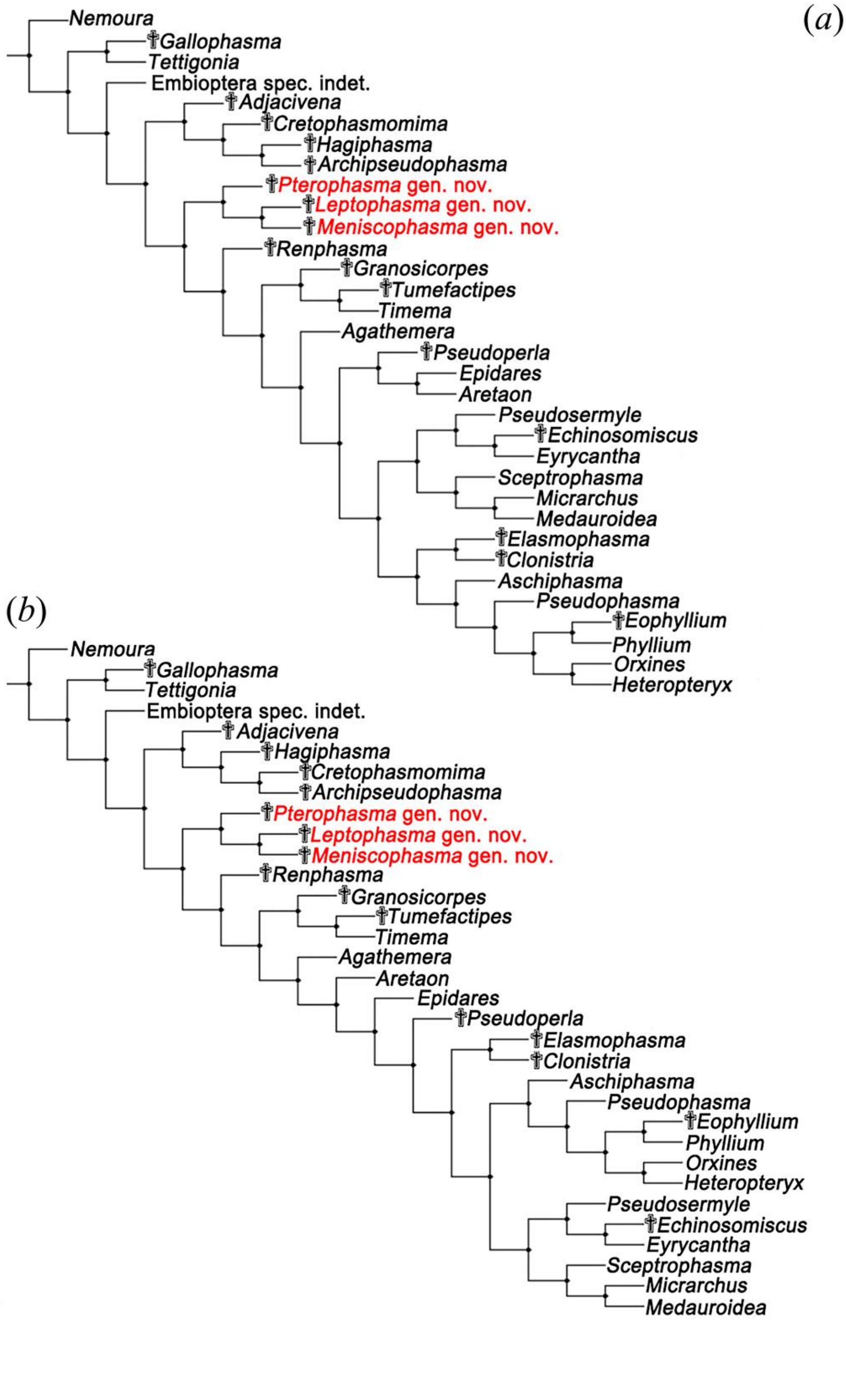

Figure S3. Supporting values of strict consensus trees. (*a*) Bootstrap supporting values are represented as numbers under the branch nodes (data in blue); (*b*) Bremer supporting values are represented as numbers on the branch nodes (data in purple).

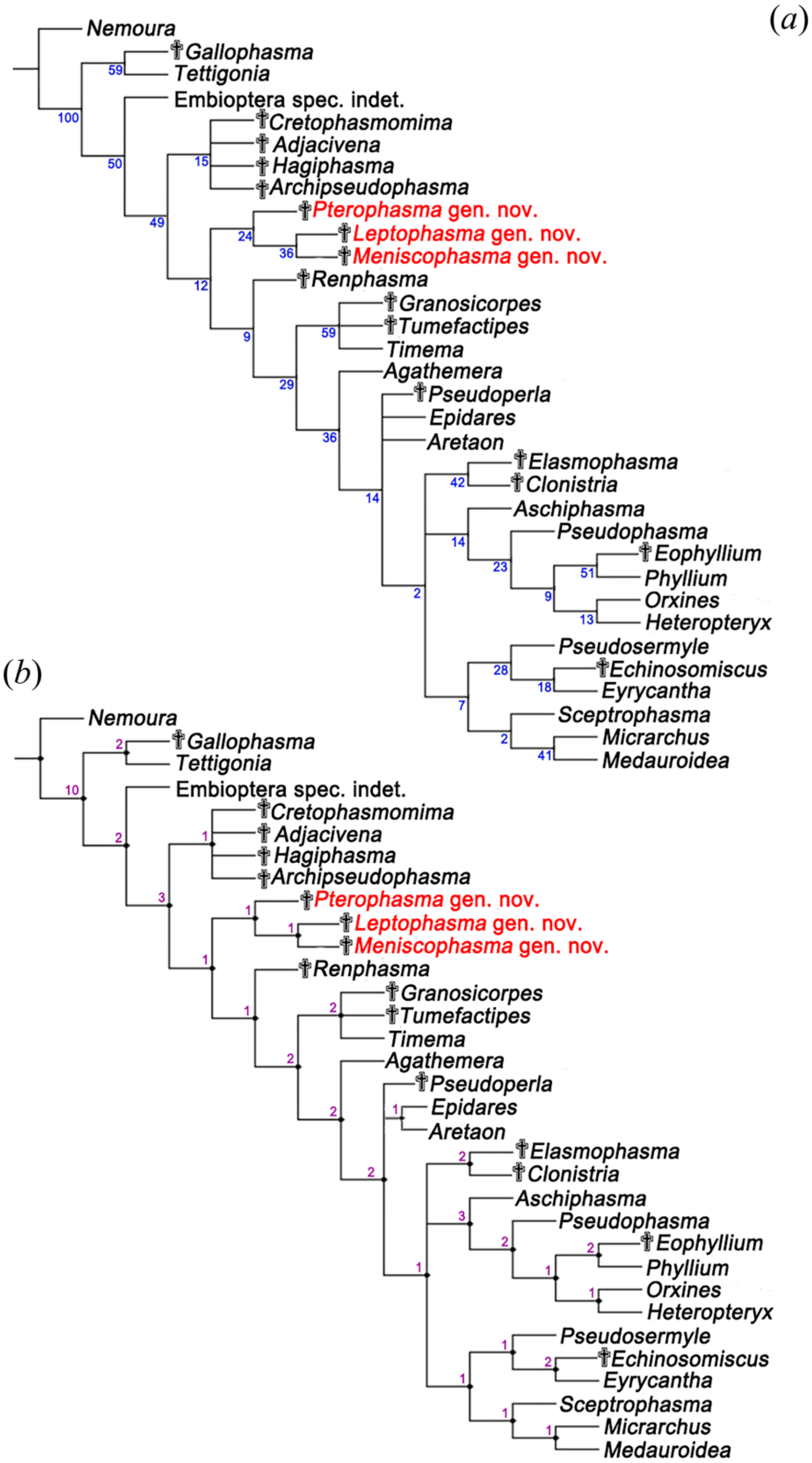

Figure S4. *Heteropteryx dilatata* Parkinson, 1798

Figure S5. *Sipyloidea amica* Bei-Bienko, 1959

Data S1. *Pterophasma erromera* Yang, Shih, Ren & Gao gen. et sp. nov.

Description. Fully winged male (figure 2a, b); whole body covered with numerous setae; head ovoid in dorsal view, prognathous; three ocelli present in vertex; compound eyes subglobose, exophthalmic; antennifer well-defined; antenna filiform, bearing numerous setae, distinctly longer than profemur, with a prominence on surface of pedicel base (figure 2c); right antenna with 13 antennomeres as preserved; scape cylindrical, longer than wide; pedicel cylindrical, shorter and thinner than scape; first flagellomere shorter than scape and pedicel combined; left antenna with only one scape as preserved (figure 2e); labrum emarginated (figure 2g); maxillary palps pentamerous, with numerous setae; cervix not preserved.

Prothorax slightly shorter than meso- and metathorax; pronotum rectangular, longer than width, no extension of the lateral margin; apertures of prothoracic defensive glands not clear due to preservation, distinctly transverse furrows on anterior part of pronotum (figure 2e); meso- and metathorax covered with wings; metasternum distinctly fused with abdominal sternum I.

Tegmina (figure 5f) slightly shorter than hind wings at rest; with the pronounced 'knob-like dorsal eversion' (figure 2d); without 'procostal' area; area between costal margin and ScP wide in proximal part; ScP about 5.4 mm long as preserved, parallel and close to RA; RA single and straight; RP with two branches, forking at about two third of wing length; MA and MP single; CuA+CuPaα with two distal branches; CuPaβ and CuPb single and straight respectively; two anal veins present, anal area with many cross-veins.

Hind wings extending beyond tegmina at rest (figure 2a, b), with the distal portion not covered by tegmina, wing venation not clear due to overlapping.

Fore and middle legs much shorter than hind legs, metafemora thicker and stronger than pro- and mesofemora; all femora round in cross section; profemora straight (figure 2a, b); trochanter small and tightly connected with femur; all tibiae round in cross section, with Y-shaped area apicalis but without spines (figure 2h); with a spine at the base of hind tibia (figure 2a, b); basitarsus elongate, but shorter than remaining tarsomeres combined; all tarsi five-segmented, with large arolia and euplantulae (figure 2h); left foreleg and hind leg not preserved.

Abdomen ventrally with a longitudinal median carina, lateral edges obvious; eleven abdominal segments preserved (figure 2a, b); segments II–VII of similar length and width; segment VIII shorter than segment VII; abdominal stigmata VIII moving back to the middle of the segment; segment X longer than segment IX, apex cleft into two lobes medially, thorn pads on the hind margin, with only two teeth on either side (figures 2f and 6a, b); epiproct and paraproct apparently (figures 2f and 6c); subgenital plate splitting into two parts transversally (figure 6a, b, denoted in blue and purple), apical part with two lobes (figure 6a, b, denoted in purple), reaching the base of segment X; two phallomeres broad and lamelliform (figure 6a, b, denoted in yellow); cerci bifurcated in basal position, outside one straight, thickened at the base and tapered toward the apical, inside one curved inward, cylindrical, both un-segmented, circular in cross section, with abundant elongated setae (figure 6a, b, c).

Measurements (in mm): body 17.34 (excluding antennae); head 2.11; right antenna (as preserved) 11.87; scape 0.52, pedicel 0.42, flagellomeres I–V 0.78, 0.48, 0.69, 0.88, 0.90, VI–VIII 1.10, IX–XI 1.30; prothorax 1.78; mesothorax 2.26; metathorax 3.22; tegmina 12.80; abdomen 8.85; profemur 2.72, protibia 2.25, protarsus 2.03, mesofemur 2.44, mesotibia 2.02, mesotarsus 1.83, metafemur 5.21, metatibia 4.97, metatarsus 2.76.

Data S2. *Leptophasma physematosa* Yang, Shih, Ren & Gao gen. et sp. nov.

Description. Fully winged male (figure 3a, b); whole body covered with numerous setae; head ovoid in dorsal view, prognathous; ocelli absent; compound eyes subglobose, exophthalmic; antennifer well-defined; antenna filiform, with 12 antennomeres as preserved, bearing numerous setae and distinctly longer than profemur; scape large and swollen in terminal, longer than pedicel and first flagellomere combined; pedicel cylindrical, longer than first flagellomere; first flagellomere longer than second and third flagellomeres; other flagellomeres gradually extending; labrum emarginated; maxillary palps pentamerous; labial palps trimerous (figure 3c).

Prothorax longer than head; pronotum rectangular, length twice as width, the first quarter prominent, no extension of the lateral margin (figure 3c); prothoracic defensive glands not clear; mesothorax and metathorax elongate and longer than prothorax; metasternum distinctly fused with abdominal sternum

I.

Tegmina (figure 5e) without ‘procostal’ area; with the ‘knob-like dorsal eversion’; area between costal margin and ScP wide in proximal part; ScP extending to middle of the tegmina, parallel and close to RA; RA with two distal short branches; RP forking at about three quarters of wing length, with two distal branches; the branch location of M distal to RP origin; MA and MP single; CuA+CuPaα with two long branches; CuPaβ and CuPb single and straight respectively; an anal vein present, anal area narrow.

Hind wings extending beyond tegmina at rest (figure 3a, b), with the distal portion not preserved, wing venation not clear due to overlapping.

All legs slender, fore and middle legs shorter than hind legs; all femora round in cross section; profemora slightly curved near base (figure 3c, arrow); trochanter small and tightly connected with femur; all tibiae round in cross section, with Y-shaped area apicalis but without spines (figure 3d, arrows); basitarsus elongate, but shorter than remaining tarsomeres combined; all tarsi five-segmented and with arolia (figure 3e).

Abdomen ventrally without a longitudinal median carina, lateral edges obvious; nine abdominal segments preserved (figure 3a); segments II–VI of similar length and width; segments VII–VIII shorter than segments II–VI; segment IX incompletely preserved; abdominal stigmata VIII not clear.

Measurements (in mm): body 17.97 (excluding antennae); head 1.51; antenna (as preserved) 7.29; scape 0.75, pedicel 0.36, flagellomeres I–X 0.33, 0.27, 0.24, 0.44, 0.59, 0.65, 0.79, 0.88, 1.01, 0.98; prothorax 1.83; mesothorax 2.29; metathorax 3.36; tegmina 13.55; abdomen (as preserved) 9.97; profemur 2.64, protibia 1.98, protarsus 2.19, mesofemur 2.71, mesotibia 2.17, mesotarsus 1.92, metafemur 5.62, metatibia 3.96, metatarsus 2.59.

Data S3. *Meniscophasma erythrosticta* Yang, Shih, Ren & Gao gen. et sp. nov.

Description. Fully winged male (figure 4a, b); whole body covered with short setae; head subglobose, prognathous; three ocelli present in protuberance of the head; compound eyes ovoid, exophthalmic; antennifer well-defined; antenna filiform, bearing numerous setae, much longer but slightly shorter than body, with a prominence on inner surface of pedicel base; left antenna incompletely preserved; right antenna with 22 antennomeres; scape cylindrical, longer than wide; pedicel shorter than scape, cylindrical; first flagellomere longer than pedicel, shorter than scape and pedicel combined; flagellomeres 4–11 of similar length; flagellomeres 11–20 of similar length and longer than all other flagellomeres; labrum emarginated; maxillary palps pentamerous, with numerous setae; labial palps trimerous, bearing numerous setae (figure 4c).

Prothorax shorter than head; pronotum rectangular (figure 4c), slightly longer than width, no extension of the lateral margin; prothoracic defensive glands not clear due to preservation; mesothorax longer than prothorax; metathorax longer than pro- and mesothorax; abdominal sternum I associated with metasternum not clear due to preservation.

Tegmina (figure 5g) slightly shorter than hind wings at rest; with the ‘knob-like dorsal eversion’; without ‘procostal’ area; area between costal margin and ScP wide in proximal part; ScP parallel and close to RA; RA single; RP unbranched, forking from RA at the one third of wing length; branches of M rather long, bifurcating distal to RP origin; MA and MP single; CuA + CuPaα with two long branches; CuPaβ single and straight; CuPb incompletely preserved; an anal vein visible, anal area without cross-veins.

Hind wings extending beyond tegmina at rest (figure 4a, b), with the distal portion not covered by tegmina, wing venation not clear due to overlapping.

Fore and middle legs shorter and thinner than hind legs; all femora round in cross section, with regular red spots (figure 4g, h, arrows); trochanter small and tightly connected with femur; profemora straight; femora of hind legs slightly curved apparently; all tibiae round in cross section, with Y-shaped area apicalis but without spines (figure 4f, arrows); all tarsi five-segmented, basitarsus slightly elongate; arolia present (figure 4d, f); left midleg and protarsus not preserved.

Eleven abdominal segments preserved, lateral edges obvious, segments I-VII covered by wings (figure 4a, b); segments VIII and IX of similar length and width; abdominal stigmata VIII not clear; abdominal tergum X splitting into two parts, crescent-shaped, extended and curved inward respectively, thorn pads present on the hind margin, with only one tooth on either side (figure 6e, f); epiproct and paraproct apparently (figure 6g); subgenital plate splitting into two part transversally (figure 6e, f, denoted in blue and purple), apical part with two lobes (figure 6e, f, denoted in purple); two elongated phallomeres beyond the tergum X (figure 6e, f, denoted in yellow); cerci bifurcated at the middle position, 1.5 mm long and 1.3 mm long respectively, un-segmented, circular in cross section, bearing abundant elongate setae (figure 6e, f, g).

Measurements (in mm): body 10.23 (excluding antennae); head 1.16; antenna 9.25; scape 0.39, pedicel 0.18, flagellomeres I 0.37, II 0.19, III 0.32, IV–X about 0.40, XI–XX about 0.50; prothorax 0.94; mesothorax 1.32; metathorax 1.47; tegmina 8.21; abdomen 6.29; profemur 1.92, protibia 1.56, protarsus 1.43, mesofemur 2.15, mesotibia 1.62, mesotarsus 1.13, metafemur 3.69, metatibia 3.11, metatarsus 1.58.

Table S1. Definition of characters and their states.

No.	Characters and their states
1.	Labrum: 0 - not emarginated; 1- emarginated.
2.	Antennifer: 0 - vestigial; 1- well-defined.
3.	Antenna of female: 0 - longer than profemora; 1 - shorter than profemora.
4.	Antenna of male: 0 - longer than profemora; 1 - shorter than profemora.
5.	Scape of antenna: 0 - large and swollen; 1 - not swollen.
6.	Galealobulous: 0 - absent; 1 - present.
7.	Lacinia: 0 - with two apical teeth; 1 - with three apical teeth.
8.	Cervix: 0 - membranous; 1 - with two lateral plates or a median plate; 2 - gula.
9.	Lateral cervical sclerites: 0 - undivided; 1 - bipartite.
10.	Prothorax: 0 - with lateral extension; 1 - without lateral extension.
11.	Defensive glands of prothorax: 0 - absent; 1 - present.
12.	Profurca: 0 - available; 1 - largely reduced.
13.	Pro- and Mesospina: 0 - present; 1 - absent.
14.	Anapleurite and coxopleurite of prothorax: 0 - separated; 1 - fused.
15.	The sensory areas of prosternum or profurcasternum: 0 - absent; 1 - present.
16.	Episternum of mesothorax: 0 - undivided; 1 - divided.
17.	Metanotum and abdominal tergum I: 0 - separated; 1 - fused.
18.	Metasternum and abdominal sternum I: 0 - separated; 1 - fused.
19.	Forelegs: 0 - short; 1 - slender, but shorter than body; 2 - as long as or longer than body.
20.	The base of profemora: 0 - straight; 1 - curved.
21.	Metafemora of the males: 0 - not or only slightly stronger than the other femora; 1 - conspicuously thickened and reinforced.
22.	Trochanter: 0 - movably detached from the femur; 1 - fused with the femur.
23.	Lateral lamellae of thorax and abdomen: 0 - absent; 1 - present.
24.	Lateral lamellae of femur and tibia: 0 - absent; 1 - present.
25.	Area apicalis of protibiae: 0 - present; 1 - absent.

26. Area apicalis of meso- and metatibiae: 0 - present; 1 - absent.

27. Area apicalis: 0 - membranous; 1 - partly sclerotised; 2 - completely sclerotised.

28. Spines of area apicalis: 0 - absent; 1 - present.

29. Tarsus: 0 - $<$ 4 articles; 1 - $\geq$ 4 articles.

30. Probasitarsus: 0 - shorter than the next four tarsomeres together; 1 - as long as or longer than the next four tarsomeres together.

31. Spines of body: 0 - absent; 1 - present.

32. Wings: 0 - present; 1 - absent.

33. Position of tegmina in mesothorax: 0 - in the basal half of mesothorax; 1 - in the distal half of mesothorax.

34. 'Knob-like dorsal eversion' of tegmina: 0 - absent; 1 - present.

35. Tegmina of females: 0 - well-developed, reaching the end of abdomen; 1 - shorter, not reaching the end of abdomen; 2 - absent.

36. Hind wings of females: 0 - well-developed, reaching the end of abdomen; 1 - shorter, not reaching the end of abdomen; 2 - absent.

37. Tegmina of males: 0 - well-developed, reaching the end of abdomen; 1 - shorter, not reaching the end of abdomen; 2 - absent.

38. Hind wings of males: 0 - well-developed, reaching the end of abdomen; 1 - shorter, not reaching the end of abdomen; 2 - absent.

39. Area between costal margin and ScP in proximal part: 0 - wide; 1 - narrow.

40. R of tegmina: 0 - branched; 1 - unbranched or without R.

41. RP of tegmina: 0 - three or more than three branches; 1 - two branches; 2 - unbranched.

42. Branch location of RP: 0 - in proximal of RP origin; 1 - in distal of RP origin.

43. M of tegmina: 0 - three or more than three branches; 1 - two branches; 2 - unbranched or without M.

44. Branch location of M: 0 - basal to RP origin; 1 - distal to RP origin.

45. Cu of tegmina: 0 - more than three branches; 1 - three branches; 2 - less than three branches.

46. Anal veins of tegmina: 0 - two or more than two anal vein; 1 - one anal veins.

47. Anal area: 0 - wide; 1 - narrow.

48. R of hind wing: 0 - branched; 1 - unbranched or without R.

49. RP of hind wings: 0 - branched; 1 - unbranched.

50. Branch location of R: 0 - in proximal of tegmina; 1 - in distal of tegmina.

51. M of hind wings: 0 - three or more than three branches; 1 - two branches; 2 - unbranched or without M.

52. Cu of hind wing: 0 - branched; 1 - unbranched or without Cu.

53. MP ending in Cu of hind wing: 0 - present; 1 - absent.

54. Anal field of hind wing: 0 - present; 1 - absent.

55. 2–7A of hind wing: 0 - without a common origin at the wing base; 1 - with a common origin at the wing base.

56. Cerci: 0 - single; 1 - bipartite.

57. Cerci: 0 - segmented; 1 - un-segmented.

58. Cerci: 0 - circular in cross-section; 1 - flatted or flatted at the base, thickened toward the apical.

59. Sternum VIII (operculum) of females: 0 - short, not covering the ovipositor valves; 1 - long, at least beyond the ovipositor valves.

60. Gonapophyses VIII: 0 - available; 1 - reduced.

61. Gonapophyses IX: 0 - available; 1 - reduced.

62. Gonoplac: 0 - present; 1 - absent.

63. Length of ovipositor: 0 - not protruding the abdomen end; 1 - gonapophysis VIII or all ovipositor strongly elongated.

64. Abdominal stigmata VIII: 0 - near the anterior border; 1 - moved back to the middle of the segment.

65. Subgenital plate (abdominal sternum IX) of the males: 0 - undivided; 1 - divided transversally.

66. Gonopods (gonostyli) of male: 0 - present; 1 - absent.

67. Genitalia (phallic organ of abdominal segment IX): 0 - symmetric; 1 - asymmetric.

68. Abdominal tergum X of males: 0 - undivided; 1 - split.

69. Thorn pads of tergum X in males: 0 - absent; 1 - present.

70. Tergal thorn fields of males: 0 - ventrally or medioventrally directed; 1 - after inside against each other.

71. Vomer: 0 - absent; 1 - present.

72. Cerci of males: 0 - straight; 1 - curved, crescent shaped.

73. Thorns of cerci in males: 0 - absent; 1 - present.

Table S2. Character state matrix of 73 characters for the 33 taxa included in the phylogenetic study.

Taxa/ character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Nemoura	0	0	0	0	1	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tettigonia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Embioptera spec. indet.	0	1	0	0	1	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Timema	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0
Agathemera	1	0	0	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	0	1	0	0
Aretaon	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	?	1	1	0	1	0	1	0	0
Aschiphasma	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0
Epidares	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	?	1	1	1	1	0	1	0	0
Eyrycantha	1	0	0	0	1	1	1	2	1	1	1	1	1	1	0	0+1	1	1	0	0	0+1	1	0	0
Heteropteryx	1	0	0	0	1	1	1	0	1	1	1	1	1	1	0	?	1	1	1	0	0	1	0	0
Medauroidea	1	0	1	1	1	1	1	2	1	1	1	1	1	1	0	1	1	1	2	1	0	1	0	0
Micrarchus	1	0	1	1	1	1	1	1+2	1	1	1	1	1	1	0	1	1	1	2	1	0	1	0	0
Orxines	1	0	0	0	1	1	1	2	1	1	1	1	1	1	0	1	1	1	2	1	0	1	0	0
Phyllium	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1
Pseudophasma	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0
Pseudosermyle	1	0	0	0	1	1	1	2	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0
Sceptrophasma	1	0	1	1	1	1	1	2	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0
Echinosomiscus	?	?	?	0	?	?	?	?	?	1	?	?	?	?	0	?	1	?	0	1	1	?	0	0
Clonistria	?	?	0	0	1	?	?	?	?	1	?	?	?	?	?	?	0	?	2	1	0	?	0	0
Pseudoperla	?	?	0	0	1	?	?	?	?	1	1	?	?	?	?	?	1	?	1	1	1	?	0	0
Elasmophasma	1	?	?	0	1	?	?	1	1	1	1	1	1	?	1	?	0	1	2	1	0	1	1	1
Tumefactipes	?	?	0	0	0	?	?	?	?	1	?	0	0	?	0	?	0	1	0	0	0	1	0	0
Granosicorpes	?	?	0	0	0	?	?	?	?	1	?	?	?	?	0	?	0	1	0	0	0	1	0	0

Gallophasma	?	?	0	0	1	?	?	2	?	0	?	?	?	?	?	?	1	?	0	0	1	?	0	0
Eophyllium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0
Archipseudophasma	?	?	0	0	1	?	?	?	?	1	?	?	?	?	?	?	?	?	1	0	0	?	0	0
Pterophasma gen. nov.	1	1	?	0	1	?	?	?	?	1	?	?	?	?	?	?	?	1	0	0	1	1	0	0
Meniscophasma gen. nov.	1	1	?	0	1	?	?	?	?	1	?	?	?	0	?	?	?	?	1	0	0	1	0	0
Leptophasma gen. nov.	1	1	?	0	0	?	?	?	?	1	?	?	?	0	?	?	?	1	1	1	0	1	0	0
Renphasma	?	?	?	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	0	0	?	0	0
Hagiphasma	?	?	0	0	1	?	?	?	?	1	?	?	?	?	?	?	?	?	1	0	0	?	0	0
Adjacivena	?	?	?	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0
Cretophasmomima	?	?	0	0	1	?	0	?	?	1	?	?	?	?	?	?	?	?	1	0	?	?	0	0

Taxa/ character	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Nemoura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tettigonia	1	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Embioptera spec. indet.	0	0	0	0	0	0	0	1	0	0	2	2	0	0	1	0	2	-	1	1	1	1	0	0	1
Timema	0	0	0	0	0	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Agathemera	0	0	1	0	1	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Aretaon	0	0	2	1	1	0	1	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Aschiphasma	0	0	2	0	1	1	0	0	1	-	2	0	2	0	-	-	-	-	-	-	-	-	-	0	1
Epidares	0	0	2	0	1	0	1	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Eyrycantha	1	1	-	-	1	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Heteropteryx	0	0	2	1	1	0	1	0	1	1	1	1	1	0	0	0	1	0+1	1	0+1	1	1	1	0	1
Medauroidea	1	1	-	-	1	1	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Micrarchus	1	1	-	-	1	1	1	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Orxines	1	1	-	-	1	1	0	0	1	-	1	1	1	1	-	-	-	-	-	-	-	-	-	1	-
Phyllium	0	0	2	1	1	1	0	0	1	1	0	1	1	0	0	0	2	-	2	-	2	1	1	0	1
Pseudophasma	0	0	2	0	1	1	0	0	1	1	1	0	1	0	0	1	-	-	2	-	2	1	1	1	-
Pseudosermyle	1	1	-	-	1	1	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Sceptrophasma	1	1	-	-	1	1	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Echinosomiscus	1	1	-	-	1	0	1	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Clonistria	?	?	?	?	1	1	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Pseudoperla	0	0	?	0	1	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Elasmophasma	0	0	?	0	1	1	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Tumefactipes	0	0	?	0	0	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Granosicorpes	0	0	?	0	0	0	0	1	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-
Gallophasma	1	1	-	-	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?
Eophyllium	?	?	?	?	?	?	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?

Archipseudophasma	1	1	?	?	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Pterophasma gen. nov.	0	0	?	?	1	0	0	0	0	1	?	?	0	0	0	0	1	1	1	1	0	0	0	?	?
Meniscophasma gen. nov.	0	0	?	?	1	0	0	0	0	1	?	?	0	0	0	0	2	-	1	1	0	1	1	?	?
Leptophasma gen. nov.	0	0	?	?	1	0	0	0	0	1	?	?	0	0	0	0	1	1	1	1	0	1	1	?	?
Renphasma	?	?	?	?	1	0	0	0	0	?	?	?	0	0	0	0	1	1	1	1	0	0	0	?	?
Hagiphasma	1	1	-	-	1	0	0	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
Adjacivena	?	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Cretophasmomima	?	?	?	?	?	?	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1

Taxa/ character	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Nemoura	1	0	0	-	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	-	0	0	0
Tettigonia	0	0	0	-	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	-	0	0	0
Embioptera spec. indet.	0	1	0	-	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	-	0	0	0
Timema	-	-	-	-	-	-	0	1	1	0	0	0	1	0	0	1	1	1	0	0	-	1	1	0
Agathemera	-	-	-	-	-	-	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0	1	0	0
Aretaon	-	-	-	-	-	-	0	1	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Aschiphasma	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1
Epidares	-	-	-	-	-	-	0	1	1	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0
Eyrycantha	-	-	-	-	-	-	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0
Heteropteryx	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Medauroidea	-	-	-	-	-	-	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0	0
Micrarchus	-	-	-	-	-	-	0	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0
Orxines	-	2	1	1	1	-	0	1	0	1	0	0	0	1	0	1	1	1	0	1	0	1	0	0
Phyllium	1	1	1	0	0	1	0	1	1	0	0	0	1	0	0	1	1	1	0	0	-	1	0	0
Pseudophasma	-	1	1	1	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0
Pseudosermyle	-	-	-	-	-	-	0	1	0	0	0	0	0	0	1	1	1	1	0	0	-	0	1	1
Sceptrophasma	-	-	-	-	-	-	0	1	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0
Echinosomiscus	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	1	1	1	0	0	0
Clonistria	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?
Pseudoperla	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0
Elasmophasma	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0
Tumefactipes	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0
Granosicorpes	-	-	-	-	-	-	0	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0
Gallophasma	?	?	?	?	?	?	0	0	0	?	0	0	?	1	?	?	?	?	?	?	?	?	0	0
Eophyllium	?	?	?	?	0	?	0	1	0	?	?	?	?	?	?	?	?	1	?	1	?	1	0	?

Archipseudophasma	?	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Pterophasma gen. nov.	?	?	?	?	?	?	1	1	0	?	?	?	?	?	1	1	1	0	1	1	1	0	0	0
Meniscophasma gen. nov.	?	?	?	?	?	?	1	1	0	?	?	?	?	?	?	1	1	0	1	1	1	0	0	0
Leptophasma gen. nov.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Renphasma	?	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Hagiphasma	0	1	1	0	0	1	0	1	0	1	0	0	?	1	?	?	?	?	?	?	?	?	0	?
Adjacivena	0	1	1	?	0	?	0	1	0	1	0	0	?	1	?	?	?	?	?	1	1	?	?	?
Cretophasmomima	0	1	1	?	0	?	0	1	0	1	0	0	?	1	?	?	?	?	?	?	?	?	0	0